A Robinson Crusoe story in the fossil record: Plant-insect interactions from a Middle Jurassic ephemeral volcanic island (Eastern Spain)

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ARTICLE INFO

ABSTRACT

We present here the first record of plant-insect interactions from an ephemeral volcanic island that was placed 150 km away from the nearest continental mass. The island was formed and destroyed during the Aalenian (Middle Jurassic) in a shallow sea of the southwestern Tethyan realm corresponding today to a place located in eastern Spain. These plant-insect interactions were mainly documented in leaves of Cycadophytes (comprising both Cycads and Bennettitales), and they have been described and classified into different Damage Types (DTs) and Functional Feeding Groups (FFGs). The interactions were assigned to 11 different DTs including different types of hole feeding, margin feeding, surface feeding, piercing and sucking, mining(?), and some putative ovipositional scars. The presence of these interactions implies that the island was colonized by different groups of insects, including orders such as Coleoptera, Hemiptera, Odonata, or Lepidoptera. The low variety and incidence of interactions comparing with other Middle Jurassic plant-insect interactions assemblages indicate that the diversity of insects was not high, possibly due to the difficulty of reaching this island by various lineages, the small size of the landmass of the island, and the limited food availability (mainly Cycadophytes). Possible colonization strategies could be by atmospheric dispersion, using floating remains of plants or pterosaurs as vectors, by active flight for Lepidoptera, or by rafting and floating in marine currents for flightless or other insects.

1. Introduction

In the famous novel by Daniel Defoe (1660–1731), after being shipwrecked, Robinson Crusoe arrives on a small desert island far from the mainland, however, after a while he discovers that he is not alone and manages to adapt and survive in adverse conditions. In this work, we present the history of some insects that "shipwrecked" on a small volcanic barrier-island during the Middle Jurassic, but like Robinson they soon found food and shelter among the indigenous plants, and eventually became established, thereby colonizing the island and the ecosystem.

Plant-insect interactions are direct evidence of the ecological relationships between two of the dominant lineages in terrestrial ecosystems in the history of life, both in terms of biomass and biodiversity (Bar-On et al., 2018; Mora et al., 2011; Zhang, 2011; Roskov et al., 2013; Stork, 2018). This key point makes interactions a valuable and direct source of information, serving as a window into past relationships between insects and plants. The history of these relationships includes mutualism, commensalism, parasitism, predation, and a long and fierce coevolutionary arms race (e.g., Maron et al., 2019; McCoy et al., 2021).

The plant-insect interactions of the Middle Jurassic belong to the phase "Herbivore Expansion 3: Middle Triassic to Recent" (sensu Labandeira, 2006; McCoy et al., 2021). During this phase, herbivory would be mainly undertaken by mites, orthopteroids, hemipteroids, and early holometabolan clades (Labandeira, 2006). During the Jurassic, there was a diversification of herbivores towards host clades including cycads, bennettitaleans, and pentoxylaleans, where probable culprits for some of these plant interactions likely reflect beetle activity (Crepet, 1974;

Klavins et al., 2005; Nishida and Hayashi, 1996; Labandeira, 2006).

Plant-insect interactions from the Jurassic are quite scarce compared to those in the Cretaceous or the Cenozoic (see Table 1). Beginning in the Early Jurassic, fossil plants from sedimentary rocks of Tabbowa, Sri Lanka show a variety of evidence for plant-insect interactions from Gondwanaland (Edirisooriya and Dharmagunawardhane, 2013), representing the first such data for the period. Among other considerations, it is during this period that the bennettitaleans (cycadeoids) are particularly attacked by insect herbivores, which seem to prefer this group of plants (Alvin et al., 1967; Scott et al., 1994; van Konijnenburg-van Cittert and Schmeißner, 1999; Popa and Zaharia, 2011). On the other hand, physical defences in bennettitaleans preserved by the presence of spines or stinging trichomes are also well known and show that these plants quickly evolved means of repelling or minimizing attacks (Pott et al., 2012).

Some cases of interactions stand out from others, such as those interactions documented on broadleaved conifers from the Jiulongshan Fm. in the latest Middle Jurassic (Callovian) of China, where external feeding, piercing and sucking, galling, and oviposition have been described principally from gymnosperms (Ding et al., 2015). Also in the Middle Jurassic of China, records of oviposition on Ginkgoales have been reported (Na et al., 2014, 2018; Meng et al., 2019). In Australia, external feeding, galling, and piercing and sucking on different plant groups have been reported in the Bathonian-Callovian of the Surat Basin and the Clarence-Moreton Basin (McLoughlin et al., 2015). Additionally, evidence of oviposition, galling, and piercing and sucking in cuticles of cycads and Ginkgoales were found in the Middle Jurassic of eastern Siberia (Vasilenko, 2005; Enushchenko and Frolov, 2020). Although the scarcity of interactions during the Middle Jurassic could be due to biases in the abundance or preservation of fossils, some authors have suggested that it could be due to a low incidence of certain types of herbivory during this period (McLoughlin et al., 2015).

Regarding the Iberian Peninsula, evidence of plant-insect interactions is quite scant, limited to a few studies on Cenozoic and Cretaceous deposits (Peñalver, 1997; Peñalver and Martínez-Delclòs, 1997; Moreno-Domínguez, 2018; Estevez-Gallardo et al., 2019) and a few interactions from the Carboniferous (Van Amerom and Boersma, 1971; Castro, 1994, 1997). Hitherto, there has been no evidence of plant-insect interactions from the Jurassic of the Iberian Peninsula.

Accordingly, the objectives of the present work are to: (a) Describe the first plant-interactions from the Jurassic of Spain; (b) Interpret which groups of arthropods may have produced the different damages; (c) Infer their environmental and ecological implications in an isolated ecosystem during the Jurassic; and (d) Suggest possible strategies of dispersion and colonization of islands by herbivorous insects during that period.

2. Geological setting

The fossil site containing the plant-insect interactions is located in an outcrop next to the TE-620 road, between the localities of La Puebla de Valverde and Camarena de la Sierra (Teruel Province, eastern Spain, Fig. 1.A, B and C).

2.1. Age of the El Pedregal Formation

The age of the El Pedregal Formation has been discussed by several authors. Martínez González et al. (1996) indicate the presence of the ammonoid *Stephanoceras* 40 m above the top of the outcrop and these authors also identified several specimens of the family Parkinsoniidae (*Parkinsonia* sp.-*Garantiana* spp.) and perisphinctids (subfamily Leptosphinctinae) in the successive levels above the stratigraphical series. They argue that the genus *Stephanoceras* belongs to the middle Bajocian and the parkinsonids and perisphinctids correspond to the upper Bajocian, concluding that the extrusion of the volcanic materials was realized before the middle Bajocian. This assertion is coherent with the ages

Table 1
Selection of evidence of arthropod damage on Jurassic plants.

| Age	Geographic area	Depositional setting	Plant remains	Interactions	References
Early Jurassic	Tabbowa beds (Sri Lanka)	Continental environment?	Leaves of Gymnosperms and Pteridophytes	Margin Feeding, Hole Feeding, Mining, and Galling	Edirisooriya and Dharmagunawardhane (2013)
Hettangian (Early Jurassic)	Pflanzensandstein (Bavaria, Germany)	Coastal environment. Fluviatile deltaic succession	Leaves of Coniferales and Ginkgoales	Oviposition	van Konijnenburg-van Cittert and Schmeißner (1999)
Hettangian-Sinemurian (Early Jurassic)	Glavcina Formation, Sirinia Basin (South Carpathians, Rumania)	Continental environment. Lacustrine/fluvial setting?	Leaves of *Pterophyllum* sp. (Bennettitales)	Oviposition	Popa and Zaharia (2011)
Aalenian (Middle Jurassic)	El Pedregal Fm., Iberian Basin (Aragón, Spain)	Coastal environment. Lagoon in a volcanoclastic barrier-island.	Complete flora dominated by cycadophytes, and some fern remains	Margin feeding, Hole Feeding, Surface Feeding, Piercing and Sucking, Oviposition, and putative Mining	This study
Middle Jurassic	Prisayan Formation, Irkutsk Coal Basin (Siberia, Russia)	Continental environment	Ginkgoaceous leaves	Oviposition, Piercing and Sucking and Galling	Enushchenko and Frolov (2020)
Callovian (Middle Jurassic)	Jiulongshan Fm. (Inner Mongolia, China)	Continental environment. Deposition within low-energy lacustrine settings.	Leaves of *Anomozamites villosus* (Bennettitales)	Margin Feeding	Pott et al. (2012)
Callovian (Middle Jurassic)	Jiulongshan Fm. (Inner Mongolia, China)	Continental environment. Lacustrine/fluvial setting	Broadleaved conifers	External Feeding, Piercing and Sucking, Galling, and Oviposition	Ding et al. (2015)
Callovian (Middle Jurassic)	Jiulongshan Fm. (Inner Mongolia, China)	Continental environment. Lacustrine/fluvial setting	Ginkgoalean leaves and seeds	Oviposition	Na et al. (2014, 2018); Meng et al. (2019)
Early, Middle and Late Jurassic	Different basins (Australia)	Continental and Coast environments	Pteridophytes and Gymnosperms	External Feeding, Oviposition, Mining, Piercing and Sucking, and Galling	McLoughlin et al. (2015)
Late Jurassic-Early Cretaceous	Doroninskoe Formation, (Transbaikalia, Russia)	Continental environment	Coniferous and ginkgoaceous leaves	Oviposition and Galling	Vasilenko (2005)
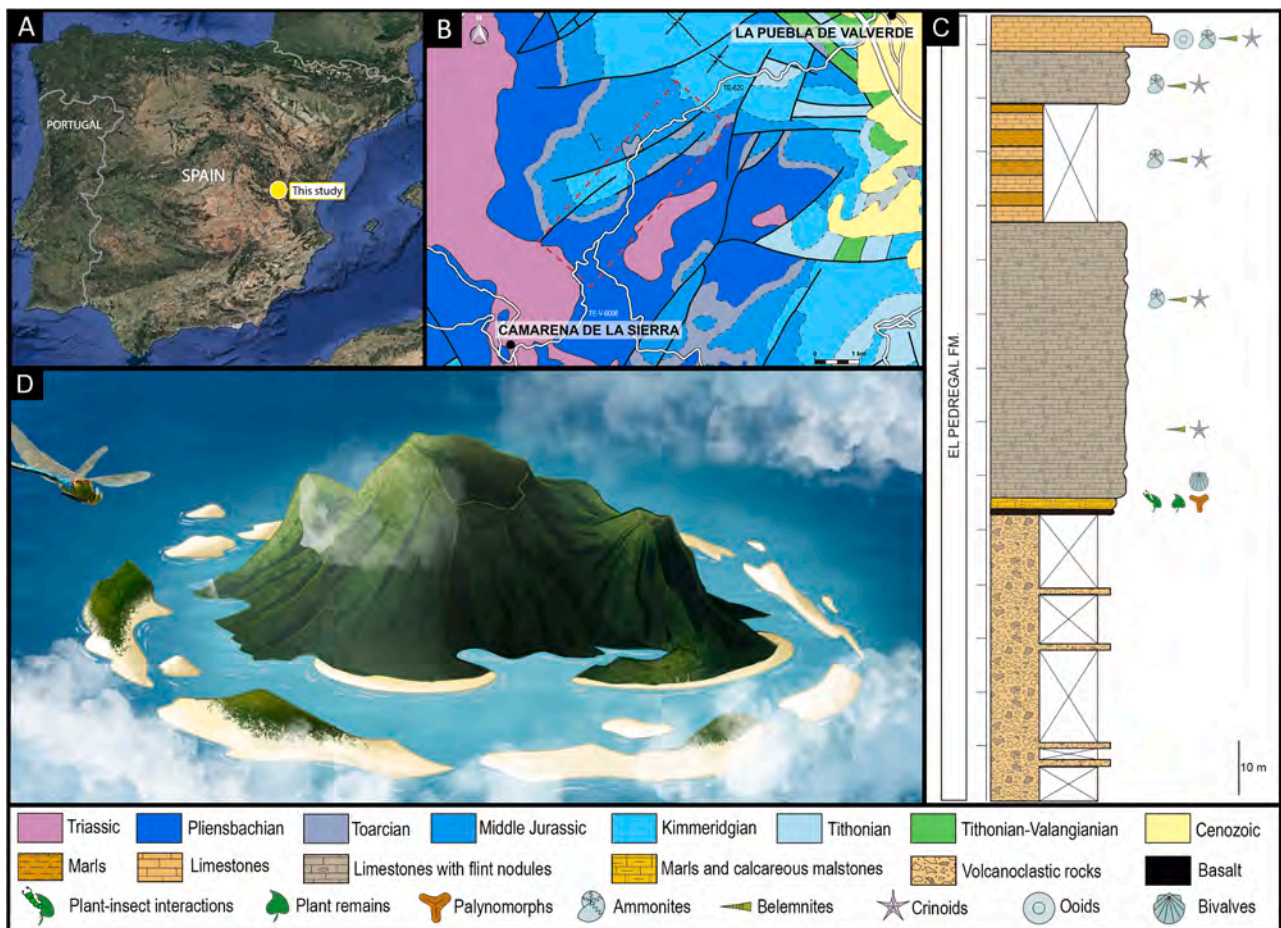
Fig. 1. A and B. Geographic and geological map of Camarena outcrop; C. Lithostratigraphic column from the studied section with the position of the plant-insect interactions, based on data from Martínez González et al. (1996), Cortés and Gómez (2018), and field observations. Scale bar = 10 m; D. Reconstruction of the landscape of the barrier-island (Artist: Juan Molina).

assigned to the El Pedregal Formation by Gómez (1979). More recently, the age of this formation was narrowed to between the chronozone *Concavum* of the upper Aalenian and the chronozone *Discites* of the lower Bajocian (Cortés and Gómez, 2016). According to Cortés and Gómez (2018) the emergence of the volcanic pile that represents the first event of volcanic island development, as well as the colonization of the emerged land by the plant community, took place in the Aalenian between the *Murchisonae* and part of the *Bradfordensis* chronozones, corresponding to a window of less than 500,000 years.

The fossils studied were found in volcanoclastic sediments of the El Pedregal Formation (Iberian Basin), dated as Middle Jurassic (Aalenian) based on ammonoids and palynology (Cortés and Gómez, 2018; Cortés, 2019; Santos et al., work in progress). During the early Aalenian, the Iberian Peninsula was a large island bathed by the proto-Ligurian Tethys Sea (Schettino and Turco, 2009, 2011; Cortés, 2019), in this shallow sea 150–200 km from the mainland, an ephemeral and relatively small island emerged due to underwater volcanic activity and volcanoclastic sedimentation, which was soon colonized by cycadophytes, some ferns, and fungi (Cortés and Gómez, 2018; Cortés, 2019; Santos et al., work in progress).

2.2. Environmental setting

El Pedregal Formation (Iberian Basin) is part of the Chelva Group (previously, the Chelva Formation.). Gómez et al. (2003) reorganized the lithostratigraphic units of the Toarcian and Aalenian stages changing the rank of Chelva Formation to Chelva Group (Gómez and Fernández-López, 2004). The El Pedregal Fm. corresponds to the lower micritic unit

of the middle part of the Chelva Fm. (Gómez and Fernández-López, 2004; Gómez, 1985). This geological formation consists of mudstone limestones and wakestone limestones of microfilaments with echinoderms and pellets, which may have intercalations of marls (Gómez and Fernández-López, 2004). The plant-insect interactions occur in the "Facies D" of Sections PV.4–10 to PV.4–13 (sensu Cortés and Gómez, 2018; Cortés, 2019). "Facies D" is composed by low-energy sediments – mainly marlstones and siltstones – with some marine bivalves and plant remains (Cortés and Gómez, 2018).

According to the sedimentological interpretation of Cortés (2019), during the Aalenian as volcanic land emerged, confined lagoon environments – not too extensive or deep – were formed and protected from oceanic waves. The sediments of these lagoons were predominantly carbonated and mixed with fine particles containing the plant fossils that preserve the interactions (Cortés, 2019; Santos et al. work in progress). The separation between the lagoons and the open sea would have been produced by the volcanoclastic deposits that acted as a barrier. Outside this volcanoclastic barrier, banks of oysters were formed, which were dismantled during stormy episodes and then dragged towards the lagoon areas where sometimes they also occur interspersed with plant remains (Cortés, 2019).

The nearest continental masses in relation to this barrier-island system were the Catalan Massif, about 150 km northeast of the island, and the Iberian Massif 200 km west of the island (Gómez and Goy, 2005; Gómez and Fernández-López, 2006; Cortés and Gómez, 2018).

The stratigraphical levels containing the palaeobotanical remains (plants and fungi) are found mixed with fossils of marine organisms such as tiny shells of bivalves, small-sized brachiopods bearing smooth and

striated shells, regular echinoderms, medium- to large-sized trochoid and turbinate gastropods, and algal remains (Cortés and Gómez, 2018; Cortés, 2019; Santos et al. pers. obs.)

The El Pedregal Fm. developed in an environment corresponding to an external marine platform, shallow, with normal salinity and occasionally affected by the action of storms. Locally, the volcanoclastic deposits occur interspersed with carbonated sediments, which are representative of confined marine shallow environments. At the top of the unit, the notable change in the characteristics of the deposits – tending to a height increase of marine carbonated deposits – show a general deepening stage due to an intense marine pulse, which is due to the development of a passage between the Proto-Atlantic Ocean and the Western Tethys during the Aalenian (Gómez and Fernández-López, 2004).

During the late Toarcian, Aalenian, and early Bajocian stages the sedimentary environment evolved into a shallow external marine platform with numerous local emersions (Fernández-López and Gómez, 1990). Other authors such as Gómez (1979) also argued that the sedimentation of the middle part of the Chelva Group took place in "a shallow platform of high to moderate energy, frequently within the photic zone and with local intertidal episodes." The regressive maximum would be reached during the middle Aalenian (Gómez et al., 2003). In this context of shallow external platform, an epiclastic barrier-island system emerged surrounding a volcanic island, more than 150 km from the nearest mainland, and which was colonized by a plant community (Fig. 1.D) that was preserved along with the traces of insect activity.

3. Material and methods

We analyse traces of plant-insect interactions on different fossil leaves of cycadophytes and ferns out of a total of 428 leaf remains collected from the outcrop. The plant remains are preserved as carbon film and impressions, and none of the fossils appear to preserve the cuticle. The preservation of complete leaves indicates that the transport was short, suggesting an autochthonous or parautochthonous origin of the plant fossils and of the interactions (also see Cortés and Gómez, 2018). For the study of the interactions, we have only taken into account that material with sufficient size and preservation to be able to assign it to a botanical group (ex. cycadophyte, ferns....). The fossils were prepared following standard techniques in the Department of Geosciences of Vigo University, using a micro-pneumatic hammer and sharp needles. Selected fossils were photographed in detail using a Canon EOS50D with a 60-mm macro lens, and with a Leica MC170-HD Camera attached to a Leica M205-C stereomicroscope. Some of the samples were photographed submersed in distilled H_2O to improve image contrast and quality. The fossils will be stored in the Museo Aragonés de Paleontología (Fundación Dinópolis), Teruel, Spain, and they are provisionally labelled as MAP-CA-0001a to MAP-CA-189c.

The preservation of the studied plants containing the interactions makes identification at the species-level difficult, so for prudence, for this work we have grouped the different leaf remains at a broader taxonomic level, In this way, the oryctocenoses from the studied fossil site – from now on Camarena Flora – is clearly dominated by cycadophytes, −99% of the plant remains- and the 1% are fern remains. We have followed the classification system proposed by Labandeira et al. (2007) for the identification of plant-arthropod interactions. In this system, the interactions observed on the leaves are classified into different morphotypes, named as Damage Types (hereafter DT), and then followed by an identifying number, where most of the DTs belong to certain Functional Feeding Groups (hereafter FFG). Additionally, each DT is connected to a certain degree of specialization, based on the occurrence on different host plants.

The statistical analyses were processed in R i386 3.6.0 (R Development Core Team) and R Commander. We have use codes based on Gunkel and Wappler (2015) to calculate the richness and rarefaction of

DTs and FFGs, to obtain standard deviations we relied on Heck et al. (1975). Plant-insect associations with statistical data are scarce from Jurassic deposits, which limits the options for comparisons with other floras. We have selected the association of interactions from Ding et al. (2015), based on its chronostratigraphic proximity, its geographical position (Northern Hemisphere), and because it is a flora dominated by gymnosperms (broadleaved conifers). To make comparisons between the interactions of Camarena and other Middle Jurassic plant-insect interactions, we processed the data of Ding et al. (2015) from the Middle Jurassic of China and analysed the rarefaction of DTs and FFGs following the same methodology applied to our data.

4. Results

Of the leaf remains analysed, a total of 14 specimens with clear herbivory marks (ex. with reaction rim or specific patterns) have been reported (see Table 2 and Figs. 2-4), which represents an incidence of 3.26%. All interactions were found in leaves of cycadophytes (which make up 99% of the flora) and no type of damage was identified in the remains of ferns. The most abundant DT is external damage, found in 2.6% of Camarena leaves, 0.2% showing piercing and sucking marks, 0.4% mining, and 0.6% oviposition scars. A total of 11 different DTs belonging to 6 FFGs were identified: hole feeding (DT01, DT02, DT03, DT04, DT64), margin feeding (DT12 and DT81), surface feeding (DT29), piercing and sucking (DT46), mining, and some putative ovipositions (DT76).

4.1. Description and identification of the interactions

4.1.1. Margin feeding
MZA-CA-29b: DT12. Two marginal feedings present on a cycadophyte leaf preserved as an impression (See Fig. 2.F). The two margin feedings are located on two consecutive pinnae of the leaf, and both are located in the upper middle part of the pinna. The first mark is 1.27 mm long and penetrates 0.9 mm into the pinna, traversing several nerves, has a thin dark reaction rim about 0.1 mm wide. The second mark extends 1.3 mm and penetrates about 0.3 mm into the pinna, has a thin reaction rim about 0.1 mm wide.

Table 2
Plant–insect interactions recorded in fossil plants from the barrier-island of Camarena (Middle Jurassic, Aalenian), El Pedregal Formation, Spain.

| Specimen	DTs	FFGs	Botanical Affinity
MZA-CA-15	DT12	Margin Feeding	Cycadophyte
MZA-CA-29b	DT12	Margin Feeding	Cycadophyte
MZA-CA-52a	DT12	Margin Feeding	Cycadophyte
MZA-CA-94a	DT12, DT29	Margin Feeding; Surface Feeding	Cycadophyte
MZA-CA-119b	DT12	Margin Feeding	Cycadophyte
MZA-CA-130a	DT81, DT64	Margin Feeding; Hole Feeding	Cycadophyte
MZA-CA-141a	DT12, DT76	Margin Feeding; Oviposition	Cycadophyte
MZA-CA-184	DT12	Margin Feeding	Cycadophyte
MZA-CA-05	DT04, DT03, DT02	Hole Feeding	Cycadophyte
MZA-CA-44d	DT02, DT01	Hole Feeding	Cycadophyte
MZA-CA-80	DT02	Hole Feeding	Cycadophyte
MZA-CA104a	Unidentified DT	Mining (?)	Cycadophyte
MZA-CA-57a	DT76, DT46	Oviposition; Piercing and Sucking	Cycadophyte
MZA-CA-04	DT76	Oviposition	Cycadophyte
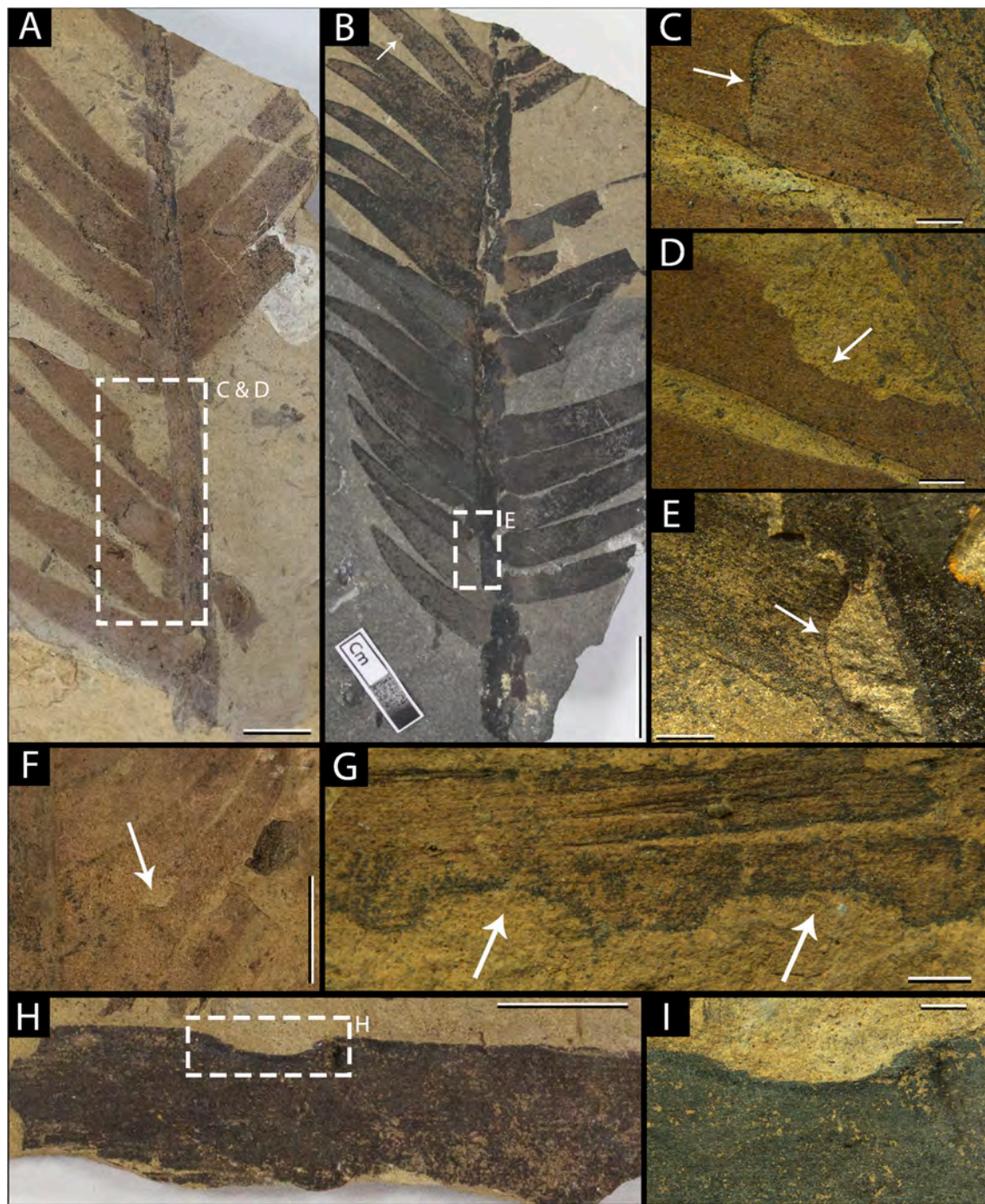
Fig. 2. A. Margin feeding pattern (DT12) and surface feeding (DT29) on the insertion of the left leaflet on specimen MZA-CA-94a. Scale bar = 0.5 cm; B. Two unidentified external damages on specimen MZA-CA-173c. Scale bar = 1 cm; C. Detail of the surface feeding (DT29) in specimen MZA-CA-94a. Scale bar = 2 mm; D. Detail of margin feeding (DT12) in specimen MZA-CA-94a. Scale bar = 2 mm; E. Detail of B, showing an unidentified margin feeding-hole feeding on specimen MZA-CA-173c. Scale bar = 2 mm; F. Margin Feeding (DT12) on leaflet of cycadophyte, sample MZA-CA-29b. Scale bar = 0.5 cm; G. Margin feeding pattern (DT12), sample MZA-CA-119b. Scale bar = 1 mm; H. Scale bars = 1 cm (H) and 2 mm (I); Margin feeding (DT12) with dark reaction rim, sample MZA-CA-52a. Scale bars = 2 mm (H) and 5 mm (I).

MZA-CA-52a: DT12. An interaction of margin feeding on the one lateral margin of a carbonized cycadophyte leaf (Fig. 2.H and 2.I). The mark is arc-shaped and 11 mm long and penetrates 1.5 mm into the pinna probably crossing some veins, although the venation is barely visible. The interaction exhibits a thickened dark reaction rim, up to 0.9 mm wide.

MZA-CA-94a: DT12 following a pattern. Two margin feedings can be seen on the upper part of two pinnae on the left side of the leaf (Fig. 2.A

and 2.D). The first interaction, located in the lower pinna, is an irregular arc with a length of 4.68 mm penetrating into the pinna up to 1.6 mm, and crossing several nerves of the pinna, although hardly any reaction rim is observed (it is not preserved or was not produced). The second interaction is an irregular arc, 5.07 mm long and 2.4 mm deep, traversing several veins and has a slight reaction rim (<0.1 mm) at the top.

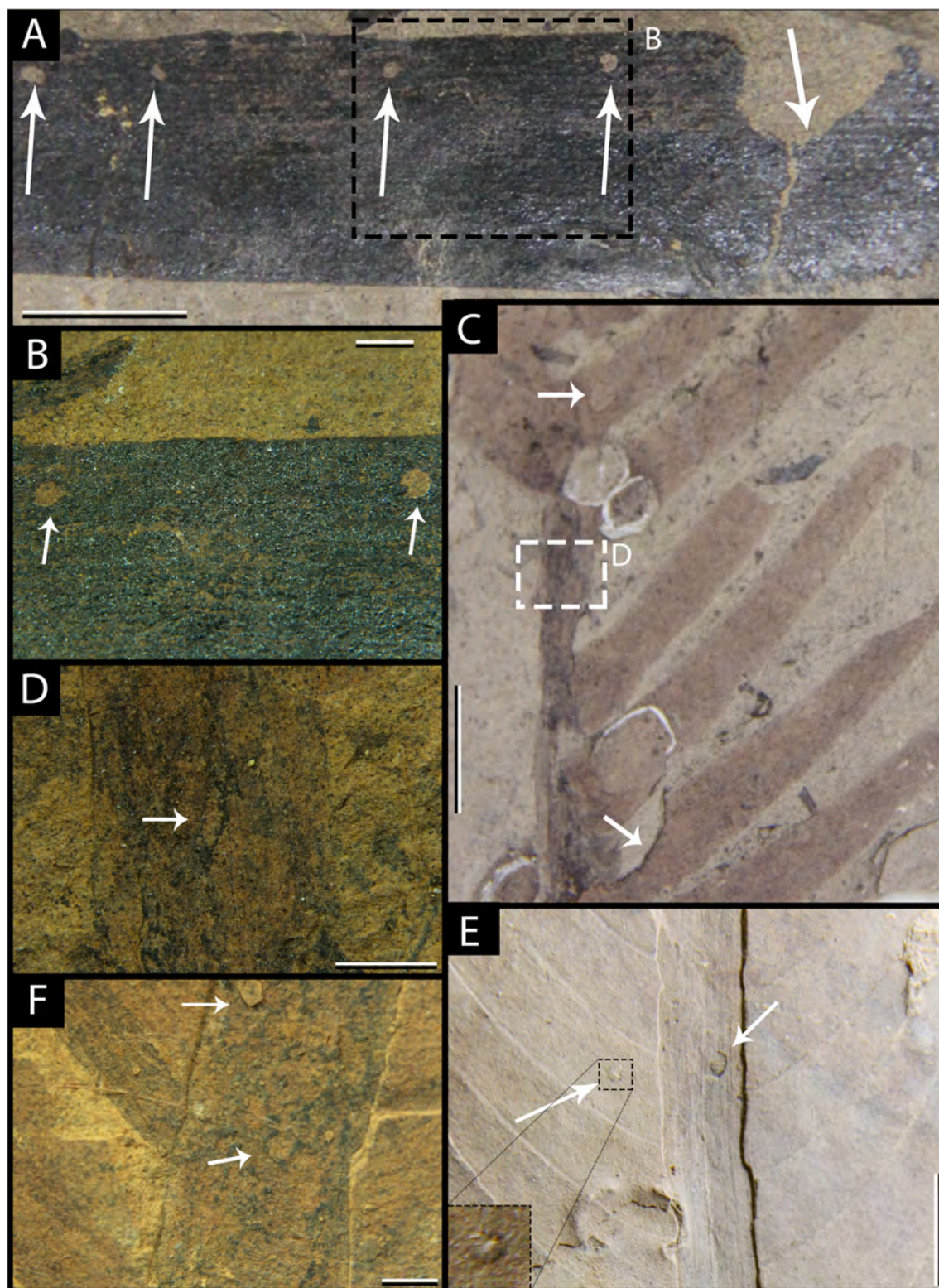MZA-CA-119b: DT12, seems to follow a pattern similar to that of

Fig. 3. A. Margin feeding (DT81) and pattern of hole feeding (DT64) on cycadophyte leaf, sample MZA-CA-130a. Scale bar = 1 cm; B. Detail of hole feeding (DT64) on specimen MZA-CA-130a. Scale bar = 2 mm; C. Margin feeding (DT12), oviposition (DT76) and possible hole feeding (white arrow in the top of the picture) on specimen MZA-CA-141a. Scale bar = 1 cm; D. Detail of the oviposition (DT76) scar on the midrib of the specimen MZA-CA-141a. Scale bar = 2 mm; E. Oviposition scar (DT76) on the midrib and piercing and sucking interaction (DT46) in a leaflet of cycadophyte, specimen MZA-CA-57a. Scale bar = 1cm; F. Two oviposition scars (DT76) on the midrib of the cycadophyte, specimen MZA-CA-04. Scale bar = 2 mm.
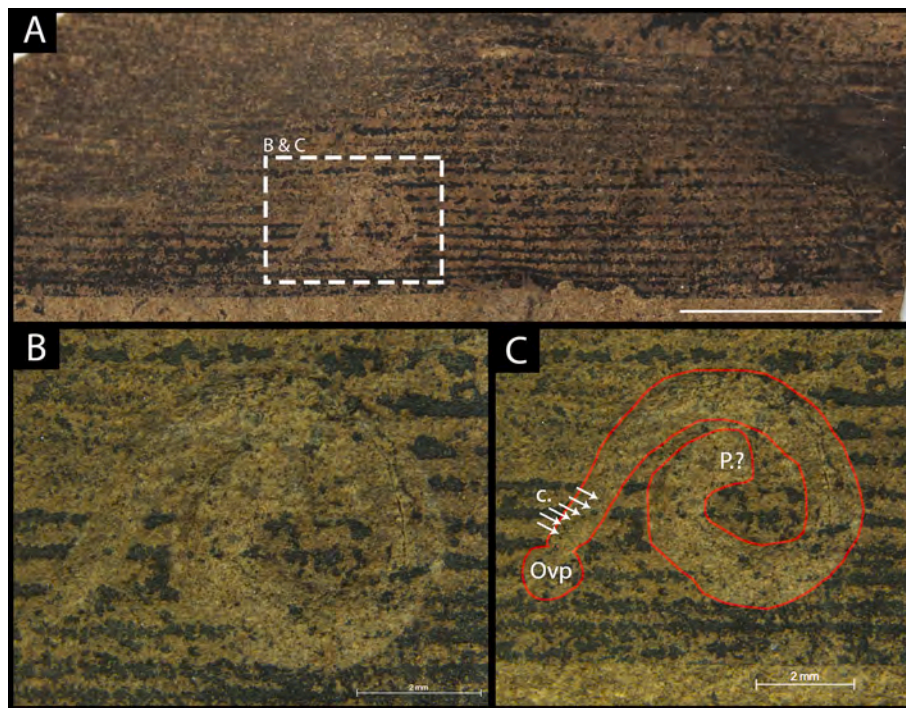
Fig. 4. A-C. Detail (A and B) and interpretation (C) of the putative mining on a cycadophyte leaf, specimen MZA-CA-104. Ovp: Oviposition scar; P.: Pupation Chamber; c.: Microcoprolites. Scale bars = 1 cm (A) and 2 mm (B and C).

DT143. A damaged cycadophyte leaf with two continuous margin feedings on its lateral margin, both arc-shaped (Fig. 2.G). The first interaction (left) is 4.2 mm long and penetrates 1.3 mm into the pinna, crossing several nerves and the putative reaction rim is dark and extends 0.5 mm thick. The second interaction has a length of almost 6 mm long, penetrating the pinna up to 1.1 mm, crossing the venation, and showing a dark reaction rim up to 0.55 mm thick.

MZA-CA-130a: DT81. Elongated pinna with different interactions, including two continuous margin feeding on its lateral margin. The first (left) is 4.5 mm long and penetrates the pinna up to 2.8 mm through several veins. The second margin feeding (right) is 3.9 mm long and penetrates up to 2 mm into the pinna through several veins. No observable reaction rim.

MZA-CA-141a: DT12. One of the segments of the cycadophyte leaf has a probable margin feeding on its inner margin (Fig. 3.C), the interaction is 9 mm long and reaches a depth of about 4.9 mm in the pinna through several veins. A slight reaction rim is present.

MZA-CA-184: DT12. Margin feeding in an elongate cycadophyte pinna, formed as an arc on one of the sides, with a length of 8.9 mm and penetrating the pinna up to 3.4 mm through several nerves. There is a slight reaction rim about 0.1 mm.

MZA-CA-15: DT12. At least two marks of marginal herbivory are seen on a carbonized cycadophyte leaf. The interactions are present on one of the lateral margins of the leaf and are arranged continuously. The first interaction is an irregular arc shape, it is about 26.5 mm long and penetrates about 6 mm (into the interior of the pinna), crossing several veins. The second mark has an arc shape, with a length of 11.16 mm and penetrates between 2 and 3 mm, crossing some nerves. Both interactions show in some areas a dark reaction rim between 0.1 and 0.2 mm wide.

4.1.2. Hole feeding

MZA-CA-130: DT64. On the margin of the pinna of a cycad leaf, four aligned hole feedings are observed following a particular distribution pattern (Fig. 3.A and 3.B). The hole feedings range from circular to slightly oval between 0.5 and 1 mm in diameter. The reaction rim is barely observable, and some hole feeding seems to have a slight thickening around it, but the preservation does not allow it to be seen clearly. The four hole feedings are aligned, they keep almost the same distance from the leaf margin (between 0.4 and 0.6 mm) and are separated from each other from 3.1 to 6.4 mm.

MZA-CA-05: DT04, DT03, and DT02. Leaf fragment of a cycadophyte with several apparent hole feedings of variable size and circular to ellipsoidal in shape, reaching 3.9–6 mm. They preserve a slight reaction rim up to 0.2 mm thick. The presence of an elongate hole feeding that crosses several nerves is remarkable. It is not fully preserved and measures more than 1 mm long, with a width of up to 0.8 mm, with a dark reaction rim of about 0.2 mm.

MZA-CA-44d: DT01, DT02. Hole feeding in a pinna of a cycadophyte leaf. It is poorly preserved as an impression with a thin patina of coal. It shows a clear hole feeding and some possible DT01 and DT02 feedings. The clearest of them is slightly irregular and ellipsoidal in shape, 1.4–0.7 mm in size and has a dark reaction rim of about 0.1 mm.

MZA-CA-80: DT02. Two hole feedings in a small fragment of a parallel-veined cycadophyte pinna of a leaf. Partially preserved as an impression with a thin patina of coal. The largest interaction is semi-circular in shape with dimensions of 2.1–1.9 mm in diameter and it appears to have a slight thickening around it, which could correspond to the reaction rim, up to 0.4 mm thick. The second hole feeding is circular, 1.1–1.2 mm in diameter.

4.1.3. Mining

MZA-CA-104a: Putative mining interaction on a cycadophyte pinna of a leaf (see Fig. 4). The gallery presents a putative spiral structure, covering an area of approximately 6.5–5 mm. The gallery begins on the left with a rounded structure that would correspond to the oviposition mark. It consists of a rounded-shaped structure with a diameter of 1.1–1.2 mm. From the oviposition mark, a spiral gallery arises, increasing in width towards the centre of the spiral due to the growth of the larval producer. The width of the gallery varies from 0.54 mm at the beginning to 1.1 mm in its final part. The final zone probably corresponds to the pupation area, but the poor preservation prevents a detailed description. Small black dots (from 0.05 mm to 0.15 mm in size)

are observed along the gallery (see white arrows in Fig. 3.C), which would correspond to the microcoprolites left by the larva along the gallery. In some parts of the mine, especially in the initial zone, the microcoprolites are aligned in a regular pattern.

4.1.4. Oviposition

MZA-CA-57a: DT76. Two egg-shaped structures appear in the midrib of a cycadophyte leaf with dimensions of 1.61–2.37 mm and 1.94–1.32 mm (Fig. 3.F). Both structures are situated in the right central part of the rachis of the leaf, keeping a distance with the closest margin of the vein of 1.60 and 1.66 mm, respectively.

CA-141: DT76. In the rachis of a cycadophyte leaf preserved as an impression with some traces of carbonization, an egg-shaped structure appears, about 1.2–0.5 mm in size (see Fig. 3.C and 3.D). The egg-like structure is adhering to the almost exact centre of the rachis of the leaf, separated by less than 2 mm from both sides of the rachis. The oviposition mark has a dark reaction rim around 0.2 mm thick.

MZA-CA-04: DT76. Two ovoid-shaped structures as impressions in the rachis of a cycadophyte leaf, with some remains of organic matter preserved as a crust of coal (see Fig. 3.E). The first scar is located in the lower part of the rachis of the leaf exhibiting a semicircular shape with approximate dimensions of 1.1–0.9 mm. The second structure is ovoid, with dimensions of 1.1–0.5 mm. Both structures are surrounded by a dark and thickened reaction rim between 0.1 and 0.2 mm wide.

4.1.5. Piercing and sucking

MZA-CA-57a: DT46. A single mark preserved as an impression located in the central and basal part on the left side of a cycadophyte pinna of a leaf (see Fig. 3.F) that would coincide with a piercing and sucking structure morphotype. It is a circular-shaped structure, 1.5–1.7 mm, showing a relief on the outside and a depression centrally. It presents a differentiated central zone up to 0.8 mm in diameter and a thickened margin approximately 0.6 mm thick.

4.1.6. Surface feeding

MZA-CA-94a: DT29. A morphotype (DT) of surface feeding appears on one of the pinnae on the right side of the leaf. It is a mark that occupies an approximate surface of 8.1–6.5 mm, located in the basal half of the pinna, which shows a more "worn" appearance than the apical half due to part of the tissue of the plant was removed (see Fig. 2.A and 2.B). The limit of the interaction is observable in the middle zone of the pinna,

where a dark-coloured black line delimits the part between the pinna affected by surface feeding and the intact part of it. This dark mark could correspond to the reaction rim and has a width of between 0.1 and 0.2 mm.

4.2. Statistics and comparations

The rarefaction curves for the plant-interaction assemblage (Fig. 5 and Fig. 6.A-C) show that due to the number of specimens sampled, 428 leaves or leaf fragments, the curve for FFGs tends to stabilize. However, both the rarefaction curve for DTs and for external damage continues to trend upward; therefore, a sampling with more leaf specimens will likely exhibit an even greater observed diversity from Camarena. The plant-insect interaction assemblage of Camarena was compared with the continental assemblage of the Middle Jurassic (Callovian) of China (Ding et al., 2015). This comparison reveals that the continental flora of China shows values of DT diversity clearly higher than those of the volcanic island of Camarena (Fig. 6.A). However, when comparing the diversity of external damage we observe quite similar values for both reservoirs (Fig. 6.C), despite both their environmental and taphonomic differences.

5. Discussion

5.1. Comparison with other Jurassic plant-insect interactions

Among the 428 leaf remains analysed for interactions, only 14 specimens have some type of clear interaction, implying a 3.26% incidence of herbivory on the Camarena flora and a total of 11 DTs. However, the rarefaction curve for all DTs (Fig. 5) shows a clear upward trend indicating that if the number of leaves sampled was higher, then it is most likely that the number of different DTs could increase significantly as is expected in this type of data (e.g., Ding et al., 2015; Gunkel and Wappler, 2015). As already mentioned, no other entire Jurassic floras have been systematically examined for plant-insect interactions. As an example, for the flora of the Jiulongshan Fm. (Callovian), Ding et al. (2015) examined a total of 88 plant specimens identifying that 33% had incidences of interaction. However, regarding the variety of DTs found, the values are relatively similar to those of Camarena, with 12 different DTs in the flora of the Jiulongshan Fm., and 11 DTs in the Camarena Flora. The low incidence of affected plants may be due to the
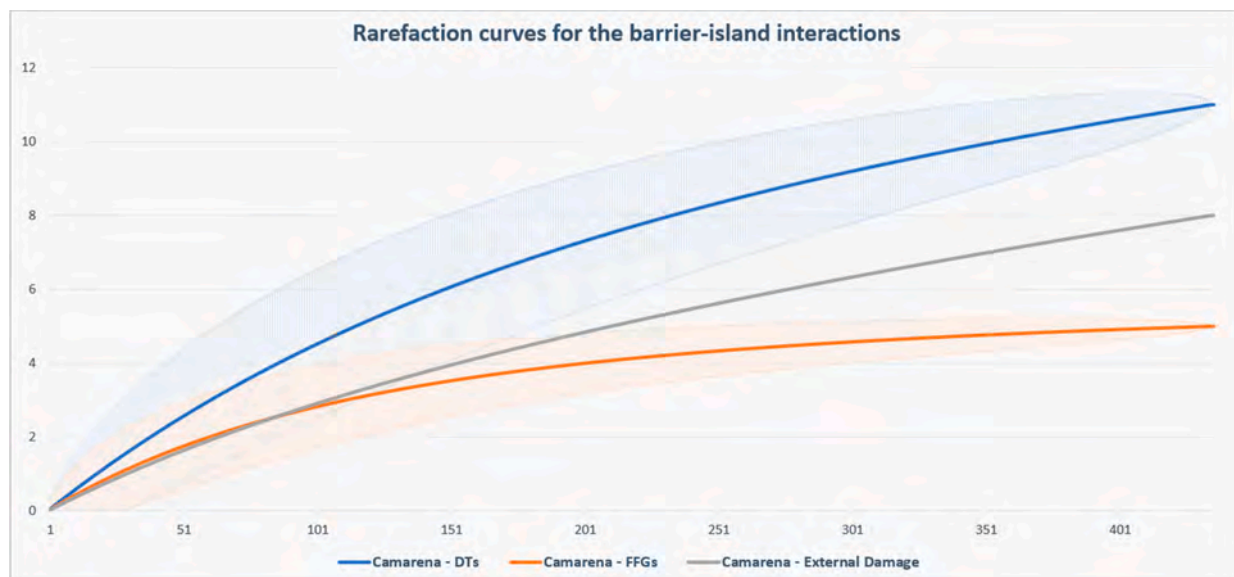

Fig. 5. Rarefaction curves for the plant-insect interactions from Camarena (Middle Jurasic, Spain) including all DTs, FFGs and External damage. The halo around each line indicates the standard deviation.
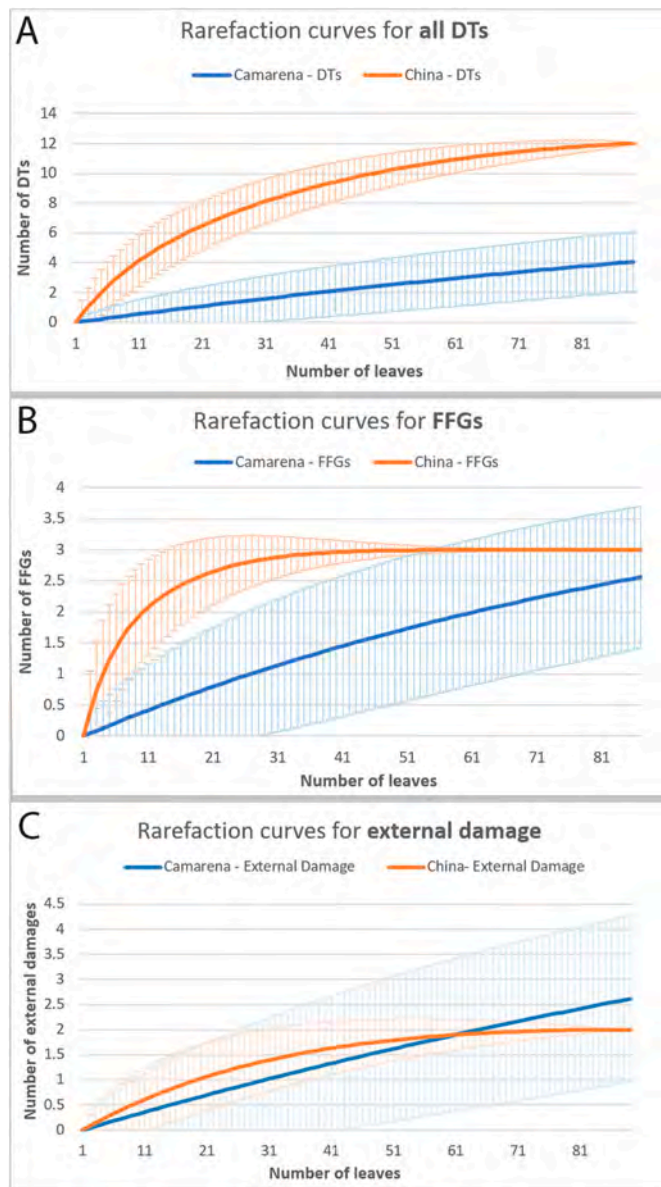
Fig. 6. A-C. Comparison between the rarefaction curves of interactions from Camarena and interactions on conifers from the Middle Jurassic of China (Jiulongshan Fm.) calculated from data of Ding et al. (2015). The halo around each line indicates the standard deviation. Note that external damage includes margin feeding, hole feeding, and surface feeding.

dominance of xerophytic species bearing thick, structurally hardened leaves and abundant development of epicuticular waxes, since in this type of vegetation lower ratios of almost all FFGs are observed (Fernandes and Price, 1992; Hanley et al., 2007; Ding et al., 2015).

It is striking that in this volcanic island the incidence of interaction is so low (3.26%) and the variety of types of damage is relatively high (11 different DTs belonging to 6 -or 5- FFGs), data comparable to that found in continental Jurassic floras (Ding et al., 2015). The number of DTs and FFGs suggests that the variety of different families of insects is relatively high (Carvalho et al., 2014), particularly if we take into account the low diversity of plants present on the island (a few species, mainly cycadophytes and ferns). However, the low incidence of plants affected by interactions would indicate that the abundance of insects was low, or that they have not fully adapted to the type of vegetation or environment, despite their taxonomic diversity.

The main food source of the studied volcanic island would be almost

exclusively cycadophytes (cycads and Bennettitales), where all the leaves found had a hard and leathery appearance that does not seem to be the best food source for insects. However, different strategies of external herbivory have been found in the interactions identified (8 DTs) including margin feeding, hole feeding, and surface feeding.

The absence of galling in the flora of Camarena could be due to the absence of gall-forming insects, which may not have been able to reach the island, or because the humidity levels on the island were exceptionally high (due to the proximity of the sea and the lagoon). In extant floras, high levels of humidity are related to lower incidences of galling as such insects prefer conditions in mid-latitude xeric environments (e. g., Fernandes and Price, 1992; Espírito-Santo and Fernandes, 2007; Espírito-Santo et al., 2007). On the other hand, Ding et al. (2015) did not report any cases of mining in the Middle Jurassic of China, even though the incidence of other FFGs was relatively high. In Camarena, despite being an isolated ecosystem, putative mining was found retaining the oviposition mark indicating that the island's environmental and ecological conditions were sufficient for some insects to complete their lifecycle (birth, growth, reproduction). The oviposition marks found on the central rachis of three specimens of cycadophyte leaves confirm that certain groups of insects were successful in completing the reproductive part of their lifecycle on the island.

Furthermore, taking into account that the plant-insect interaction assemblage of Ding et al. (2015) is located on the continent, it would be expected that its variety of DTs would be notably higher to that found in an isolated and limited environment such as that of the volcanic island of Camarena. Indeed, the comparison between the rarefaction curves of these two assemblages (Fig. 5.B-E) confirms that, with the same level of sampling, the diversity of interactions from the continent is much greater than that found on Camarena. This observation is consistent with the conclusion that only a few groups of insects managed to reach the island, thus limiting the variety of DTs and FFGs. On the other hand, the more general damages such as external damage (which could be produced by almost any order of insects) do not present significant differences between both floras (Fig. 6.C). The marked difference in the number of DTs between the continental gymnosperms of China and the insular gymnosperms of Camarena would support the hypothesis that in Camarena the distance between the island and the mainland was great, and that the existence of an 'island corridor' between the mainland and the volcanic island, and along which insects could "jump" from island to island, seems unlikely. If such an island chain was present, the richness of DTs from Camarena would be expected to be more similar to that found in other continental floras of the same age.

The interactions of Camarena are representative of "Herbivore Expansion 3: Middle Triassic to Recent" (Labandeira, 2006; McCoy et al., 2021). In this phase occur the first evidence of mining (Labandeira et al., 2018), and all FFGs are present (Labandeira, 2006; Labandeira et al., 2018; McCoy et al., 2021). The case of Camarena, despite its peculiarities, is typical of interactions of this phase, corresponding to a flora dominated by a variety of types of cycadophytes with evidence of mining and six different FFGs.

5.2. Affinities of the interactions

Several species of extant cycads have different mechanisms of defence against insect herbivory. For example, some species within genus *Zamia* L. have tough leaves, toxins such as azoxyglycoside, and trichomes (Lucas et al., 2000; Kitajima et al., 2012). The toughness of cycad leaves is considered the primary defence against herbivory (Lucas et al., 2000; Kitajima et al., 2012; Prado et al., 2014). However, the new leaves, due to their need for growth, are not yet toughened and therefore may be more susceptible to attack. It is believed that this is why some cycads evolved a synchronicity in their leaf flush, with all individuals producing their new leaves at the same time and in a short period of a few weeks, a strategy to minimize insect attack over time (Clark et al., 1992; Prado et al., 2014). Nevertheless, these strategies are insufficient

to avoid herbivory, and some species like *Zamia stevensonii* Taylor and Holzman are host to specialized leaf herbivories such as some lepidopterans of the family Lycaenidae (Lepidoptera), or beetles of the Orsodacnidae and Languriidae (Coleoptera) (Prado et al., 2014). The genus *Aulacoscelis* Duponchel and Chevrolat (Coleoptera) has been reported as a specialized consumer of cycad leaves in Australia and America (Cox and Windsor, 1999). Although *Aulacoscelis* produces different types of DTs in cycads, surface feeding stands out, in which they ingest only the epidermis of the leaf rather than the parenchyma. This type of surface feeding in cycads could be reminiscent of DT29 observed in some specimens of Camarena, where only the epidermis of the leaf was removed. This same type of damage in cycads was also found by Labandeira et al. (2002) in leaves of *Nilssonia yukonensis* Hollick in deposits of the Cretaceous-Tertiary boundary, and these authors related this type of damage with the one produced by *Aulacoscelis* in modern cycads. However, the chances that the damage to Camarena plants are produced by insects specialized to herbivorous cycads seem low, owing to both the isolation of the locality and the difficulty of insects to initially access the island. Thus, the probability of successful location and colonization by a plant specialist would be unlikely. Specialists, if encountering the island, would have a low chance of finding their specific host plant already present. It seems more likely that the damages are produced by generalist insects, which are more suitable to successful invasions of isolated habitats, and which then adapted to the dominant flora of the island to survive.

External feeding marks are also known from modern cycads (genera *Zamia* and *Ceratozamia* Brongniart) and made by caterpillars of the genus *Eumaeus* Hübner (Lycaenidae). These caterpillars consume the leaves, including the venation, of cycads in South America. Other species of the genus *Cycas* L. from Thailand and Vietnam are also found with different types of margin feeding by caterpillars of the genus *Chilades* Moore (Lycaenidae) (Marler, 2013). Various species of Lepidoptera have been reported as consumers of different genera of cycads, including the families Tineidae, Blastobasidae, Cosmopterigidae, Nymphalidae, Lycaenidae, Geometridae, and Erebidae, some of which are obligate consumers of cycads (i.e., genera *Luthrodes*, *Eumaeus*, and *Theclinesthes*) (Whitaker and Salzman, 2020). Some extant bugs (Hemiptera) also specialize on leaves of cycads, such as *Aulacaspis yasumatsui* Takagi, which in recent years has been accidentally introduced to different islands with the effect of bringing various island species of *Cycas* to the brink of disappearance in these ecosystems (Marler and Lawrence, 2012; Marler, 2013).

Considering that modern herbivores of cycadophytes are principally Lepidoptera, Coleoptera, and Hemiptera, – it is likely that these groups, especially Coleoptera and Lepidoptera, are the main producers of margin, hole, and surface feeding in the cycads of Camarena. The piercing and sucking interaction assuredly corresponds to some bug lineages (Hemiptera), with perforating and sucking mouthparts. Given their size, it is unlikely to represent the activity of thrips (Thysanoptera), even though they are often constituents of aerial plankton (Mound, 1983).

Although different orders of insects can produce mining, Hespenheide (1991) reports four main large groups as responsible for mining: Coleoptera, Lepidoptera, Diptera, and Hymenoptera. Within the Coleoptera, the main leaf-mining beetles belong to the Buprestoidea (Evans et al., 2015). The putative mine found at Camarena (Fig. 4) has a spiral pattern, where the oviposition mark is on the outside, and the larva, after hatching, followed a spiral feeding pattern towards the inside of the spiral. This type of pattern in mines is quite unusual. Currently, few insects follow this type of behaviour (some Diptera and Coleoptera), and among them the type of mining that most closely resembles that of Camarena are the mines made by *Brachys cleidecostae* Migliore et al. (2020) (Buprestidae). The mines produced by this species, although they exhibit some morphological differences, do follow a pattern remarkably similar to that of the Camarena mine. In this beetle, the larva emerges from the egg and follows a feeding pattern in a spiral

towards the interior of the spiral segment, where it builds the pupation chamber. In addition, the remains of the egg are visible even after mining (Migliore et al., 2020), as in the trace from Camarena. Although we cannot assert to which group of insects the mining interaction of Camarena belongs, we suggest that the "distinctive" pattern of the mine could link it to the Buprestoidea, a lineage that diversified and became comparatively abundant during the Jurassic (Evans et al., 2015; Pan et al., 2011). Nevertheless, the preservation of the putative mine (Fig. 4) leaves a lot of room for interpretation. Based on other geological evidence (e.g., sedimentology, depositional environment), it cannot be ruled out that the preserved structure represents a serpulid worm that has encrusted on the surface of the plant, as it appears that the curved structure is on top of the leaf rather than within the leaf. In addition, the venation of the plant is seemingly obscured but not altered by the trace as one would expect from a leaf mine.

5.3. Implications of the presence of insects: dispersion strategies

The evidence of insects on the Camarena volcanic island raises the question of how insects from different lineages managed to reach a landmass more than 150 km out to sea, and to successfully colonize the island, establishing new trophic networks with the indigenous flora (Gillespie et al., 2012). Furthermore, the low incidence of interactions on the island of Camarena suggests that interspecific and intraspecific competition between the resident herbivores was likely not considerable (e.g., Gillespie and Roderick, 2002).

One hypothesis is that some of these insects colonized the island by passively floating in air currents, as aerial plankton. Today, many different types of arthropods, particularly those that are minute to small during some phase of life, travel long distances when caught by swift air currents, sometimes attaining hundreds of meters in altitude (Hespenheide, 1977). This form of passive dispersal (i.e., movement not actively directed by the insect itself towards a specific location) could have deposited insects on Camarena island, such as small Coleoptera or Hemiptera, but is unlikely for larger insects or those that are adept and active fliers, such as Odonata, Diptera, or Lepidoptera (e.g., Ansorge, 2003).

Another dispersal strategy for the colonization of islands by insects is via rafting or floating on the surface of the sea. In the Galapagos Islands, flightless insects have been found floating in the pleustron (sea-surface) several tens of kilometers from the nearest island during episodes of El Niño, and it is even possible that several species of insects have colonized the islands using rafting or floating as a dispersal strategy (Peck, 1994). In the marine pleustron insects have been found from the orders Orthoptera, Hemiptera (specifically Heteroptera), Hymenoptera, Diptera, Coleoptera, and Psocoptera (Peck, 1994). In the Izu-Bonin oceanic Islands of Japan, there have been cases of dispersal and colonization of islands by beetles via rafting, taking advantage of the force of the Kuroshio Current, which can reach speeds up to 100 km / day (Osozawa et al., 2016). It is clear that rafting is an important factor for the passive dispersal of insects, influencing the dispersion and ultimately ecological and historical biogeography of those lineages. Although the characteristics of the currents of the Jurassic sea in which the Camarena volcanic island was situated are unknown, rafting could have been used by different insect lineages to reach the island, and depending on the speed of the currents, such insects could potentially reach the island within a few days.

The third possible strategy would be by transport on some substrate, such as logs (driftwood) or plant remains floating between landmasses. Alternatively, another mode of transport would be via an animal vector, either phoretically or accidentally. Phoresis by insects on modern flying vertebrates is common (Figuerola et al., 2003), and such an association is a potentiality during the Jurassic. Pterosaurs were the sole flying vertebrates during the timeframe of Camarena island, and it is possible some insects could travel long distances attached to hirsute bodies of pterosaurs (e.g., Haddoumi et al., 2016). Hemipterans are often

phoretic, and phoresy cannot be excluded as mechanism for their introduction to ancient islands (Williams and Miller, 2010).

The presence of lepidopteran scales in Triassic and Jurassic shallow-marine sediments has recently been reported by van Eldijk et al. (2018), and lepidopteran scales have also been found in Late Jurassic marine sediments of Spain (Santos, Diez, Wappler, personal observation). Accordingly, it seems that some primitive moths were present during the Middle Jurassic and potentially could migrate a few kilometers out to sea, as was shown for moths preserved in the Lower Eocene Danish Mo Clay (Rust, 2000). Taking this into account, it is possible that some moths managed to reach Camarena during the Aalenian by active flight, either on a single trip or aided by wind streams. Possible moth oviposition scars from Camarena are consistent with such a hypothesis, although there is the possibility these scars were produced by Odonata or Coleoptera, the former of which could have dispersed by flight, while it is less likely for the latter.

6. Conclusions

Analysis of the flora of the volcanic island of Camarena exhibits an interesting plant-insect interaction assemblage from the Aalenian (Middle Jurassic), in which at least 11 DTs belonging to 6 FFGs have been identified. These include margin feeding, hole feeding, surface feeding, piercing and sucking, and putative oviposition and mining. These interactions were probably produced by different groups of insects that managed to colonize the island, among which could be Coleoptera (Buprestidae), Odonata, Hemiptera, and Lepidoptera.

Comparison of the interactions of Camarena with interactions from other continental floras of the Middle Jurassic show that its diversity of DTs is relatively low, consistent with an isolated ecosystem such as that of Camarena, located about 150 km from the mainland. The low diversity of DTs suggests that many groups of insects could not reach the island, and that the existence of a "bridge" for dispersal via a corridor of islands connecting Camarena with the mainland is unlikely.

Due to the great distances with the closest landmasses, colonizing insects arrived at the island by accident. Among dispersal strategies compatible with the paleogeographic interpretation of the island and the inferred types of insects, passive dispersal methods such as rafting or floating, where insects would be swept into the pleustron, or flying in swift air currents, are particularly likely. Additionally, some insects could have reached the island by transport on or within some substrate, such as logs or plant remains floating between landmasses; phoretically on flying vertebrates such as pterosaurs; or even by active flight in the case of some Lepidoptera.

Declaration of Competing Interest

The authors whose names are listed immediately below certify that they have NO affiliations with or involvement in any organization or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership, or other equity interest; and expert testimony or patent-licensing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

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